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OCCURRENCE OF THE RED ALGA *THOREA VIOLACEA* (BATRACHOSPERMALES: THOREACEAE) IN THE HUDSON RIVER, NEW YORK STATE

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ABSTRACT

We discovered a population of *Thorea violacea* in the upper Hudson River of New York State during September 1994. The same site was barren of *Thorea* the following June, but two and a half months later—a year after the initial collection—a large population of thalli, some over a meter in length, was again present. This seasonality may account in part for the seeming rarity of this large, conspicuous alga. Thalli presumed to represent the Chantransia phase of the *Thorea* life cycle occurred on rocks at the same location with the same phenology. The Hudson River site represents the first confirmed North American locality of *T. violacea* north of Texas and the most northerly North American locality of the family Thoreaceae. Characterization of the chemical and physical conditions at the study site suggests broader environmental tolerances (lower specific conductance, greater water flow, colder water regimes) of this group than previously known.

Key Words: Chantransia stage, freshwater algae, Hudson River, Rhodophyta, *Thorea violacea*

INTRODUCTION

The Thoreaceae (Batrachospermales) is a family of multiaxial red algae, whose members, *Thorea* and *Nemalionopsis,* are among the largest red algae found in freshwater; *Thorea* may be up to 2 m long (Bischoff, 1965). The branched, cylindrical axes of these algae consist of an unpigmented, filamentous medulla surrounded by laterally disposed, highly pigmented filaments. Thallus color is generally blue-green or red.

Life cycles in the three families of the Batrachospermales typically involve alternation of morphologically dissimilar phases. Taxonomic diagnoses are based principally on the more conspicuous and anatomically complex gametophyte phase. This phase bears the generic epithet, e.g., *Thorea* phase. The sexual life cycle known for representatives of the Batrachospermaceae and Lemaneaceae involves an inconspicuous, freely branching, diploid phase, called Chantransia, that produces sessile, haploid gametophytes directly from apical cells following somatic meiosis (Sheath, 1984). Female gametes (carpogonia) and zygotes are re-

tained on the gametophyte, which results in the growth of diploid, spore-producing filaments, collectively termed the carposporophyte, on the female gametophyte. Diploid carpospores, released by the carposporophyte, grow into the Chantransia phase (Sheath, 1984).

Life histories of the Thoreaceae are poorly known. Sexual structures have been described for some representatives of *Thorea* (Yoshizaki, 1986; Necchi, 1987), but the location of meiosis in the life history has not yet been documented. Asexual reproduction is common and conspicuous in this family (Swale, 1963) and involves the differentiation of spores, termed monospores, from terminal cells of lateral filaments. Although the morphology of the asexually reproducing *Thorea* phase thalli resembles that of gametophytes, monospores rather than gametes are produced (Swale, 1963). Monospores are also produced by Chantransia phase thalli. Regardless of the phase that generates the monospores, all monospores grow into thalli of the Chantransia morphology (Swale, 1962). Presumably, *Thorea* phase thalli that produce monospores rather than gametes are part of an apomictic life cycle, but chromosome counts are not available to evaluate this hypothesis. Generic phase thalli of *Nemalionopsis* produce monosporangia terminally on long lateral filaments (Sheath et al., 1993). Generic phase thalli of *Thorea* produce monosporangia on short, branching, lateral filaments, and the long lateral filaments are entirely vegetative (Sheath et al., 1993).

Sheath et al. (1993) recently revised the taxonomy of the Thoreaceae, reducing the number of recognized species of *Thorea* from thirteen to four. Two of these occur in North America, most commonly in the southern United States and Mexico (Sheath et al., 1993). *Thorea hispida* (Thore) Desvaux (as *T. ramosissima* Bory and *T. andina* Lagerheim et Möbius) has been reported from Nebraska (Hedgcock and Hunter, 1899), Illinois (Tiffany and Britten, 1952), and Ohio (Hirsch and Palmer, 1958), but the most northerly confirmed site for *T. violacea* Bory de Saint-Vincent (as *T. riekei* Bischoff) in North America, until our discovery of this species in the Hudson River, was southern Texas (Bischoff, 1965; Sheath et al., 1993). We also found in the field the presumptive alternate life history (Chantransia) phase of this alga. Based on environmental conditions present at the New York site, a greater ecological and geographical range for this species and for the genus is indicated.

STUDY SITE

Thorea violacea was found growing attached to pebbles and small rocks at depths of ca. 30–70 cm in the Hudson River (73°35′W, 43°11′23″N), Saratoga County, Northumberland Township, New York State. The site is near the eastern shore of Thompson Island, downstream of a low head dam. The area containing *Thorea* was less than 1000 m^2. A portion of the site was shaded late in the day by trees onshore. *Thorea* grew in open areas between patches of vascular macrophytes, and only where the river bed consisted of pebbles and small rocks. Farther from shore, vascular macrophytes completely occupied the substratum; farther downstream, the river bed was mud rather than pebbles. *Thorea* was first discovered on 15 September 1994. Additional collections were made and environmental parameters were measured on 29 September 1994. Surface current velocity over the *Thorea* patch was 63 cm sec^{-1}. Specific conductance was 119 μS cm^{-1}; pH was 6.9; alkalinity was 0.39 meq l^{-1}. The site was revisited 30 June 1995, but no *Thorea* was detected. However, large thalli again were abundant when the site was visited 10 September 1995. Attempts to locate *Thorea* at three other relatively high-flow sites in the Hudson River and six selected tributaries in the area were unsuccessful.

Our measurements of conductivity and pH fell within the ranges recorded in unpublished US Geological Survey (USGS) data collected at Fort Edward, located 9 km upstream of our study site: conductance there was 44–136 μS cm^{-1}, and pH was 6.6–7.7. Total P was 0.1–0.5 mg l^{-1}, and NO_3^- was 0.2–0.9 mg l^{-1}. During a nine-year period, mean annual discharge ranged from 110–203 m^3 sec^{-1}, with a nine-year mean of 143 m^3 sec^{-1}. Water temperature ranged from 0–26°C; all twenty readings from November to March were less than 10°C. Five readings of water temperature during September, the month during which *Thorea* was collected, ranged from 15–19°C.

RESULTS AND DISCUSSION

Thalli of the *Thorea* phase of *T. violacea* varied considerably in the amount of macroscopically visible branching present. Most thalli were profusely branched near the base, resulting in many long axes without a distinct main axis (Figure 1); other thalli had

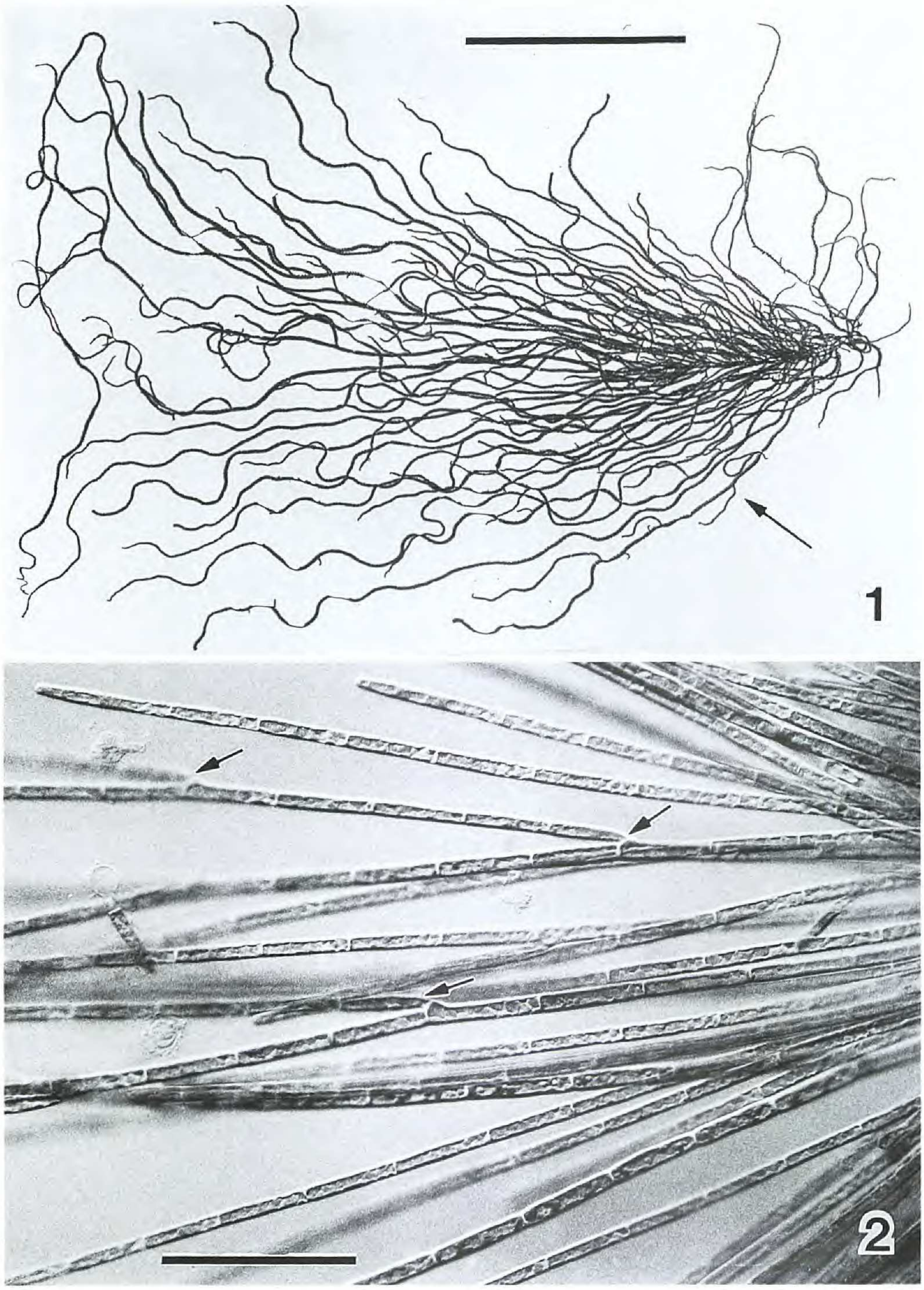


Figure 1. Herbarium specimen of monospore-bearing *Thorea* phase of *Thorea violacea* from the Hudson River. Branching is extensive near the base of the thallus, but few branches (arrow) emerge along the length of the long axes. Scale bar equals 0.1 m.

Figure 2. Light micrograph of a section of one long axis showing the distal portion of assimilatory filaments that radiate from the axis (axis not shown, but see Figure 3). Note that assimilatory filaments have non-clavate apical cells and occasional branches (arrows). Scale bar equals 100 μm.

only one or a few long axes. Secondary branching, which was initiated below the growing apices, occurred sparsely along the length of the long axes (Figure 1).

Each long axis was composed of numerous filaments whose branching was visible only by microscopic examination (Figures 2, 3). The core of the axis was composed of highly branched, interwoven, unpigmented filaments encased in a common mucilaginous matrix (Figure 3). At the outer edge of this colorless medullary zone, medullary filaments produced branches, not encased in mucilage, that were highly pigmented, occasionally branched (Figure 2), and oriented perpendicular to the axis (Figure 3). This fringe of lateral, determinate, assimilatory filaments surrounding the medulla formed a photosynthetic cortex. Monosporangia were produced on short filaments interspersed among the bases of the lateral assimilatory filaments (Figure 3).

The identity of our specimens as *T. violacea* was determined using key criteria proposed by Sheath et al. (1993): generally sparse secondary branching of long axes (Figure 1) and assimilatory filaments occasionally branched and with non-clavate apical cells (Figure 2). This identification was confirmed by Sheath (pers. comm.). Some thalli exceeded 1 m in length, but most were between 0.5–0.9 m long. Measurements of thallus features described below were made on living thalli. Long axes were 2–3 mm in diameter. Most of the diameter consisted of the lateral assimilatory filaments that arose from the tough, resilient, colorless, medullary zone, 0.5 mm in diameter. Cells of assimilatory filaments were 8–10 μm in diameter (Figure 2). Basal cells of the assimilatory filaments were 20–30 μm long (Figure 3). Within a filament, cell length increased progressively over a span of several cells, until cells attained a relatively uniform length of 42–50 μm. Although many assimilatory filaments were unbranched, a single branch was common. Lateral branches emerged from the distal portion of the cell bearing the branch, just below the crosswall (Figure 2). Filaments with as many as four branches were found. Apical cells of assimilatory filaments were cylindrical except for their rounded tips; they did not taper and were not markedly longer than other cells (Figure 2).

The only reproductive structures observed were sporangia (Figure 3), each producing a single spore. All thalli examined microscopically bore a profusion of such sporangia. These were presumed to be monosporangia, because they were borne terminally

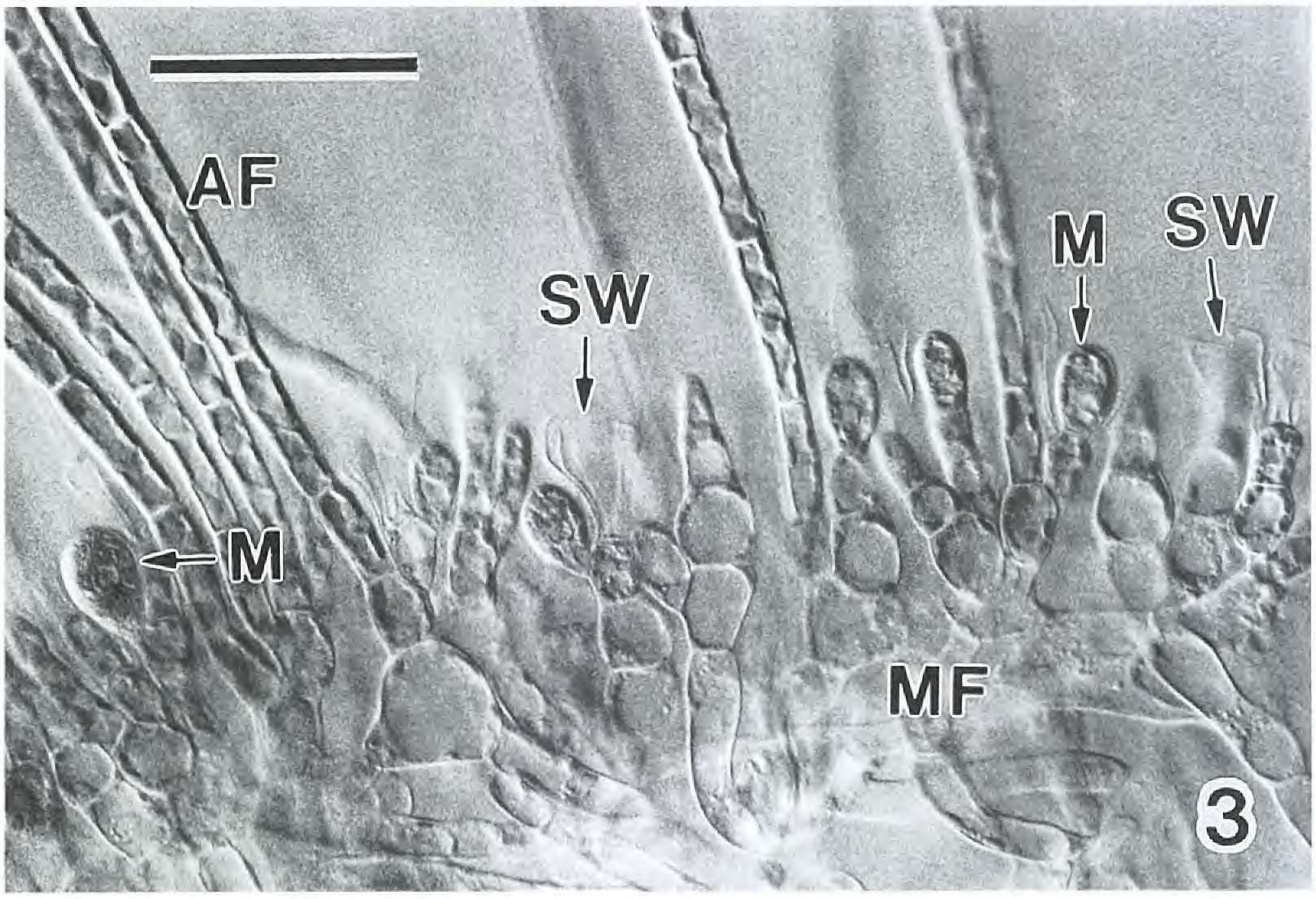


Figure 3. Light micrograph of a section of one long axis showing the outermost portion of the medullary zone and the proximal portion of the zone of pigmented cells. Branches of medullary filaments (MF) give rise to long assimilatory filaments (AF) and short filaments that produce monosporangia (M). Note empty sporangial walls (SW) of discharged monosporangia. Scale bar equals 50 μm.

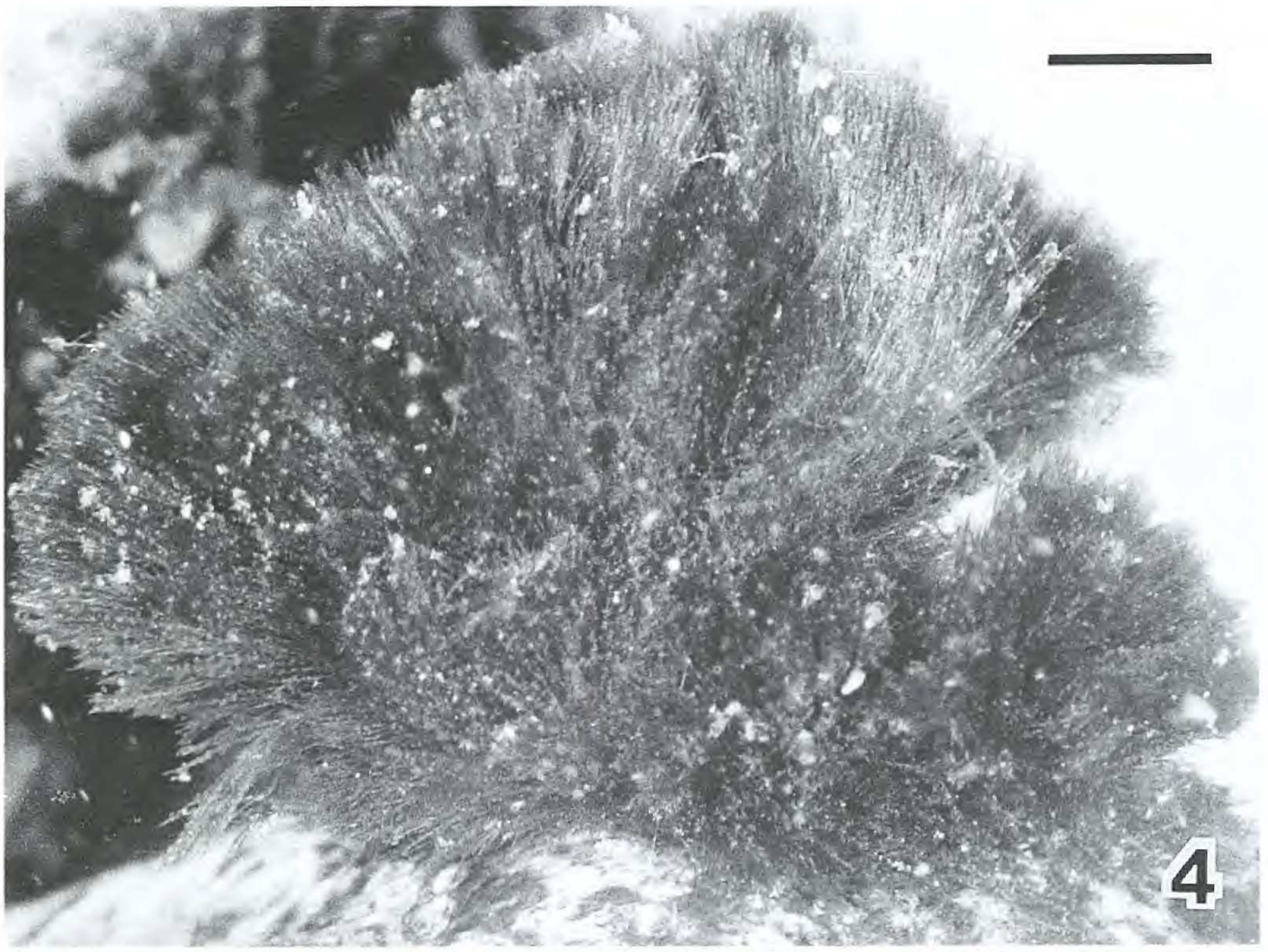
or laterally on short filaments, a few cells long, that formed a pigmented layer around the medulla (Figure 3). By contrast, carposporangia of *Thorea* (not observed) are produced on branching, multicellular filaments that originate from carpogonia, which in turn are borne on short filaments (Yoshizaki, 1986; Necchi, 1987). The total length of monosporangial filaments in our specimens was about 50–60 μm. Mature sporangia were 15–18 μm in diameter and about 25 μm long. The walls of discharged sporangia persisted (Figure 3), and thus served as a marker of post-discharge development of the subtending filament. In some filaments, the cell subtending a discharged sporangium divided to produce a new sporangium that developed within the loose confines of the old wall. Alternatively, the new apical cell was vegetative and, one or two cell divisions later, a terminal sporangium was again formed.

Specimens from the Hudson River had several features that differed from Bischoff's (1965) descriptions of *T. riekei,* which Sheath et al. (1993) placed in synonymy with *T. violacea.* Our

alga was blue-green in color, and it maintained this color upon drying. The long assimilatory filaments moved freely, and they were not encased in mucilage. Bischoff (1965) reported that the Texas specimens were generally rust-colored, and he demonstrated that the assimilatory filaments were embedded in mucilage. However, these features may be environmentally variable; Sheath (1984) noted that mucilage was not abundant in his specimens from the same location in Texas. Bischoff (1965) also reported that assimilatory filaments were unbranched and that apical cells were tapered and twice as long as other cells. Tapered apical cells of *Thorea* specimens from Texas were also noted by Hedgcock and Hunter (1899), whereas branching assimilatory filaments and cylindrical apical cells (Figure 2) were present in thalli from the Hudson River. Further study is needed to establish whether these differences are taxonomically significant.

Red algal thalli of considerably different morphology were present on rocks in the same part of the river bed. These were presumed to represent the Chantransia stage of the *Thorea* life history. Some thalli were visible only by microscopic examination of the rock surface, but a few formed grey tufts up to 9 mm in length (Figure 4). When viewed by light microscopy, chloroplast color and morphology were identical to that of the *Thorea*-phase thalli, and the pattern of lateral branch emergence was the same (Figure 5). Cells were 13–16 μm in diameter and 32–40 μm in length. Small thalli were sparsely branched, but larger ones had increasingly frequent branching towards the apices of the filaments and bore monosporangia. Two species of bluish-green *Audouinella* are recognized to occur in freshwaters of North America, and it is possible that one or both might represent life-history stages of the Batrachospermales (Necchi et al., 1993), but neither of these closely resembles the presumptive Chantransia stage present at our site.

Ours is the first report of field-collected Chantransia stage of *Thorea* in North America. As in other Batrachospermales (Sheath, 1984), thalli of the gametophyte morphology of *Thorea* are known to arise directly from the Chantransia phase (Swale, 1962; Bischoff, 1965). Monospores from both Chantransia and *Thorea* phases are known to grow into Chantransia (Swale, 1962), and carpospores produced on the *Thorea* phase are presumed to grow into Chantransia (Necchi, 1987). However, none of these links



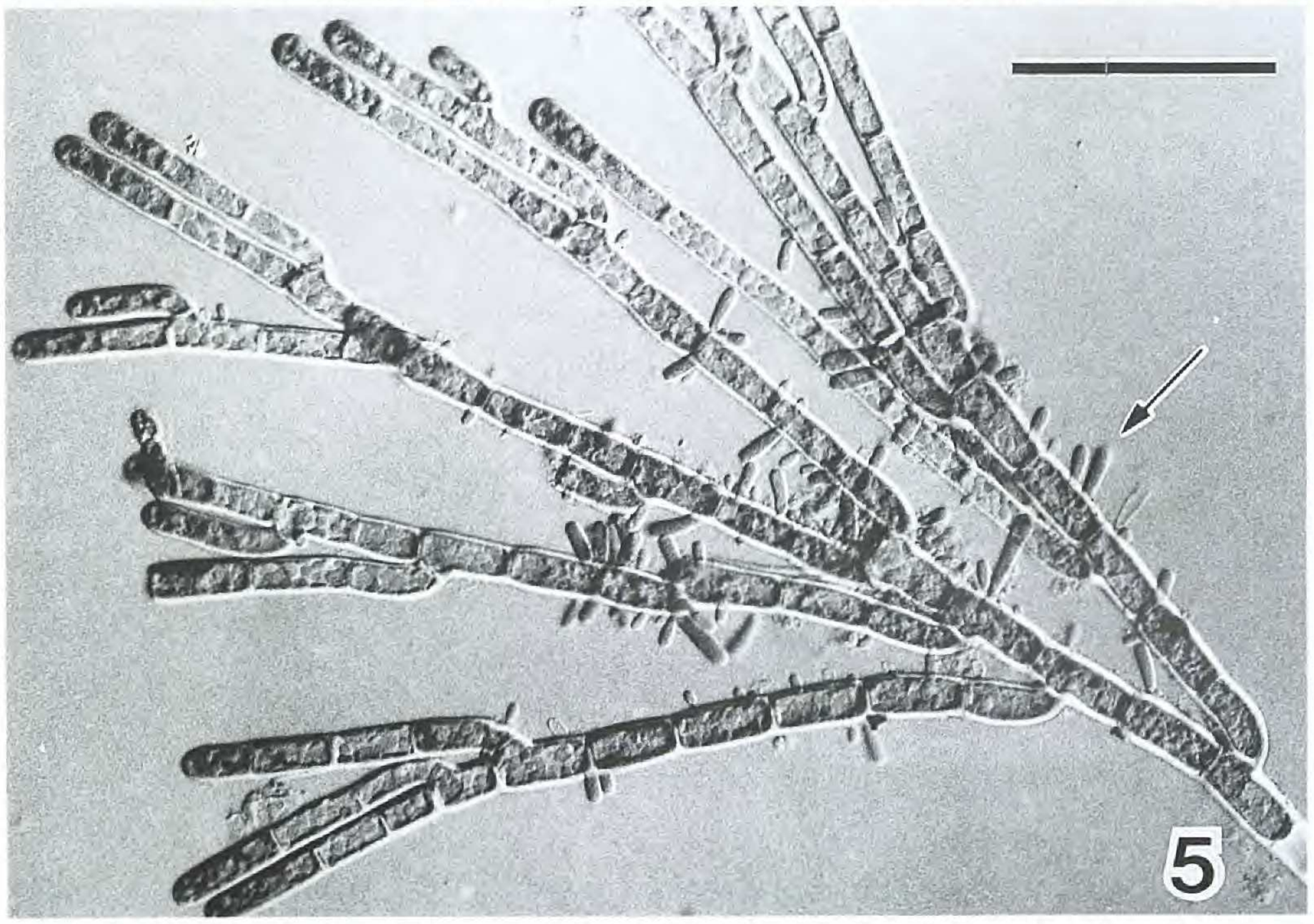


Figure 4. Putative Chantransia stage of *Thorea violacea* showing extensive branching. Scale bar equals 2 mm.

Figure 5. Light micrograph showing branching of putative Chantransia stage. Small lateral appendages (arrow) are epiphytic, unicellular blue-green algae. Scale bar equals 100 μm.

between the presumed stages of *T. violacea* in the Hudson River has been established.

In addition to the significant extension of the geographic range of *Thorea* in North America, the presence of this alga in the Hudson River represents a considerable extension of environmental conditions under which members of this family are known to grow. As summarized by Sheath et al. (1993), the Thoreaceae are found in streams with mean specific conductance of approximately 300 μS cm^{-1} (range 180–500 μS cm^{-1}), pH of 8.0 (range 7.5–8.3), current velocity of 30 cm sec^{-1} (range 9–99 cm sec^{-1}), width of 6.5 m (range 1.5–12 m), and temperature of 20°C (range 15–24°C). Our data and that of the USGS show significantly lower conductance (44–136 μS cm^{-1}), lower pH (6.6–7.7), greater than average current velocity (63 cm sec^{-1}), lower than average temperature during the month of collection (16.8°C), and larger stream size (the Hudson River dam just upstream of the *Thorea* patch is 120 m wide).

Unlike many freshwater algae, the red algae do not form thick-walled spores capable of surviving adverse conditions for long periods (Sheath and Hambrook, 1990). Therefore, annual extremes in environmental conditions, and not just the conditions during the time at which the macroscopic phase develops, must have an effect on the range of distribution of freshwater red algae. Although *Thorea* occurs at higher latitudes in England (Swale, 1962, 1963) and Germany (Schmidle, 1896; Schnepf, 1992), the Hudson River site undoubtedly experiences lower temperatures for longer periods. Water temperature measured by the USGS near the *Thorea* site was below 10°C from November to March.

The absence of *T. violacea* at our site during early summer is interesting, because *Thorea* typically grows in geographic regions of generally higher water temperatures and greater light intensity than occur in the Hudson River during early summer. Although the Chantransia stage was not detected during the early summer collection, it could have escaped detection if present as creeping filaments. The Chantransia stage is believed to be perennial (Sheath and Hambrook, 1990). Alternatively, this *Thorea* patch may be repopulated by spores from upstream populations of either phase. Spores would give rise to Chantransia, which in turn would produce the *Thorea* phase directly. The growth of *T. violacea* must have occurred in the interval between the end of June, at which time it was not detected, and mid-September, by which time some

achieved 1 m in length. Rapid growth is typical of *Thorea*. Swale (1962) found that *T. hispida* (as *T. ramosissima*) grew as much as 44 cm in one week.

It remains to be determined how far north *Thorea* may grow. The proximity of the Hudson River site to the St. Lawrence River watershed, and the connection of the Hudson River to this watershed through the Lake Champlain Canal, provides opportunity for *Thorea* to range considerably farther north. The newly recognized broader range of *Thorea*'s environmental tolerances requires rethinking of the apparent warm-temperate distribution of the Thoreaceae in North America. The more common presence of the Thoreaceae in southern locales might simply reflect slow post-glacial recolonization of former ranges from small populations in southern refugia, as was suggested by Sheath and Hambrook (1990). Three reported localities of *T. hispida* are of similar latitude and near the southern limits of glaciation (Hedgcock and Hunter, 1899; Tiffany and Britten, 1952; Hirsch and Palmer, 1958), but the specimens of *T. violacea* in the Hudson River are the first members of this family discovered deep within the glaciated region of North America.

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LITERATURE CITED

Bischoff, H. W. 1965. *Thorea riekei* sp. nov. and related species. J. Phycol. 1: 111–117.

Hedgcock, G. G. and A. A. Hunter. 1899. Notes on *Thorea*. Bot. Gaz. 28: 425–429.

Hirsch, A. and C. M. Palmer. 1958. Some algae from the Ohio River drainage basin. Ohio J. Sci. 58: 375–382.

Necchi, O., Jr. 1987. Sexual reproduction in *Thorea* Bory (Rhodophyta, Thoreaceae). Jap. J. Phycol. 35: 106–112.

———, R. G. Sheath, and K. M. Cole. 1993. Systematics of freshwater *Audouinella* (Acrochaetiaceae, Rhodophyta) in North America. 2. The bluish species. Arch. Hydrobiol./Suppl. Algol. Stud. 71: 13–21.

SCHMIDLE, W. 1896. Untersuchungen über *Thorea ramosissima* Bory. Hedwigia 35: 1–31.

SCHNEPF, E. 1992. Electron microscopical studies of *Thorea ramosissima* (Thoreaceae, Rhodophyta): taxonomic implications of *Thorea* pit plug ultrastructure. Pl. Syst. Evol. 181: 233–244.

SHEATH, R. G. 1984. Biology of freshwater red algae. Prog. Phycol. Res. 3: 89–157.

——— AND J. A. HAMBROOK. 1990. Freshwater ecology, pp. 423–453. *In:* K. M. Cole and R. G. Sheath, eds. Biology of the Red Algae. Cambridge University Press, Cambridge, England.

———, M. L. VIS, AND K. M. COLE. 1993. Distribution and systematics of the freshwater red algal family Thoreaceae in North America. Eur. J. Phycol. 28: 231–241.

SWALE, E. M. F. 1962. The development and growth of *Thorea ramosissima* Bory. Ann. Bot. (London), N. S. 26: 105–116.

———. 1963. Notes on the morphology and anatomy of *Thorea ramosissima* Bory. J. Linn. Soc., Bot. 85: 429–434 + 1 plate.

TIFFANY, L. H. AND M. E. BRITTON. 1952. The Algae of Illinois. University of Chicago Press, Chicago, IL.

YOSHIZAKI, M. 1986. The morphology and reproduction of *Thorea okadai* (Rhodophyta). Phycologia 25: 476–481.

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